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ECOLOGY OF DAPHNIA IN BULL SHOALS RESERVOIR

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RESEARCH REPORT 74

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ECOLOGY OF DAPHNIA IN BULL SHOALS RESERVOIR

By Richard L. Applegate and James W. Mullan

RESEARCH REPORT 74

UNITED STATES DEPARTMENT OF THE INTERIOR
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FISH AND WILDLIFE SERVICE
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BUREAU OF SPORT FISHERIES AND WILDLIFE
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ABSTRACT

Life histories of *Daphnia galeata mendotae*, *D. retrocurva*, *D. parvula*, *D. ambigua*, and *D. schødleri* are compared with year class strength and food of threadfin shad, *Dorosoma petenense*, in Bull Shoals Reservoir from 1965 to 1967. Maximum population density of daphnids was in April, May, and June. Populations declined to insignificant densities throughout the rest of the year. Declines coincided with inclusion of *Daphnia* in the diets of >14.0-mm threadfin shad. Declines in the summer of 1967 coincided with both young shad predation and high *Leptodora kindtii* density. Population changes associated with declining year class strength of threadfin shad were an increase of the large *D. schødleri* and *Leptodora kindtii* from nondetectable or trace densities to relatively large populations, an increase from nondetectable densities of daphnids in the summer to detectable densities, and a twofold to threefold increase in the summer standing crops of *Bosmina longirostris*.

ECOLOGY OF DAPHNIA IN BULL SHOALS RESERVOIR

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Daphnia is a primary food of planktivorous fish (Ivlev, 1961), and populations may be reduced or annihilated by predation of introduced fish (Brooks and Dodson, 1965). Although predation by invertebrates like *Leptodora* can be significant, as demonstrated by Hall (1964) and Wright (1965), the predation by fish is considered the more important.

The genus *Daphnia* of the crustacean order Cladocera, or water fleas, contains 15 North American species. Although the geographical distributions of the species overlap, Brooks (1957) points out that ability to compete successfully in different habitats determines their distribution. The ponds and small lakes in the unglaciated part of the continent have species assemblages unlike those of the large deep lakes in the glacial lake zone. The species assemblages of Bull Shoals Reservoir in the Arkansas and Missouri Ozarks suggest a succession from endemic species to populations containing both endemic species and species common to the glaciated northern latitudes (Applegate and Mullan, 1967b).

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The objectives of this report are to describe the life histories of five species of *Daphnia* in Bull Shoals Reservoir and to compare population cycles with year class strength and food habits of threadfin shad, *Dorosoma petenense* (Günther).

Bull Shoals Reservoir was filled in 1952 and is the lowermost impoundment on the White River in the Arkansas-Missouri Ozarks (fig. 1). Principal physicochemical and limnological features are presented in table 1.

Cladocera and the Limnetic Community

Of the 25 species of Cladocera (table 2) inhabiting Bull Shoals Reservoir, 15 are littoral or benthic species that rarely occur in the limnetic zone and are common prey of fish feeding in the littoral zone (Applegate and Mullan, 1967a; Applegate, Mullan, and Morais, 1966). Five of the other 10 species belong to the genus *Daphnia*.

Seasonal standing crop estimates of net plankton in Bull Shoals Reservoir have a peak density in April–May (53 mg/m^3 dry weight) and a low in August (18 mg/m^3 dry weight). Maximum densities of net phytoplankton occur in the late winter and spring and consist almost entirely of

bacillariophycean and chrysophycean species. The spring bloom is followed typically by a minor summer bloom of *Ceratium hirundinella* and *Pediastrum* species and a fall bloom of *Lyngbya birgei*.

Coinciding with and following the spring phytoplankton bloom are pulses of rotifers and crustaceans. Rotifers occur at mean densities of approximately 57/liter during the spring and maintain den-

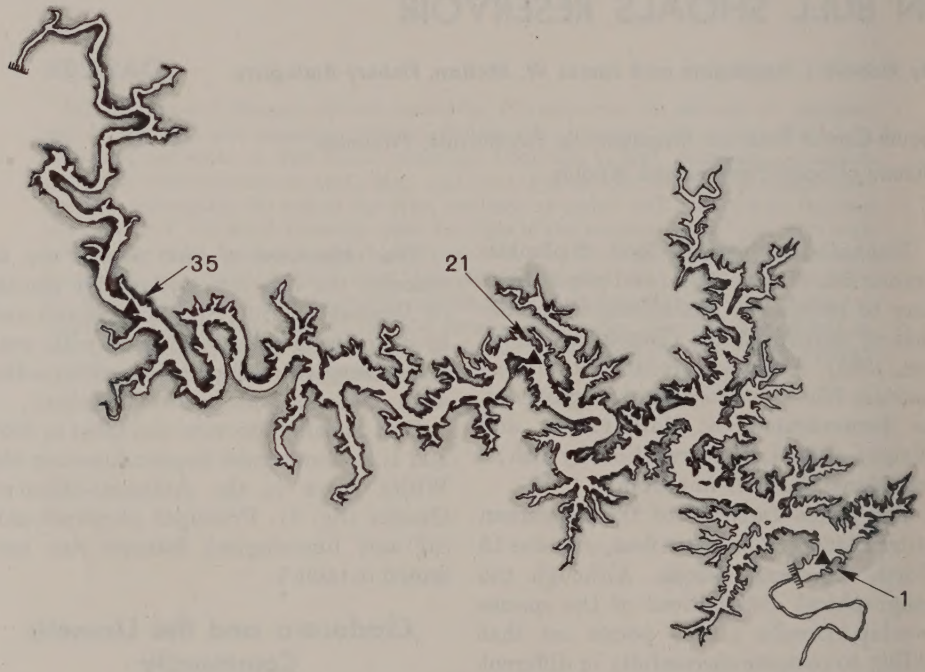

FIGURE 1.—Bull Shoals Reservoir and location of sampling stations.

TABLE 1.—*Hydrographic, physicochemical, and biological characteristics of Bull Shoals Reservoir at power pool elevation*

Item		Value
Hydrographic features:		
Elevation	(above mean sea level) meters	199.4
Area	hectares	18,400
Length	kilometers	140
Mean depth	meters	20.4
Maximum depth	meters	61.3
Shore development		24.8
Outlet depth	meters	36.3
Storage ratio	years	0.7
Storage began		1951
Physical-chemical features:		
Secchi disk transparency	meters	0.3–7 (avg >3)
pH		7.2–8.8 (avg 7.9)
Specific conductance	μmhos/cm at 25° C	220–320 (avg 275)
Bicarbonate alkalinity	milligrams per liter	165 avg
Biological features (dry weight):		
Dissolved organic matter	milligrams per liter	4.53–8.12 (avg 5.80)
Nannoseston	milligrams per liter	0.59–1.85 (avg 1.03)
Netseston	milligrams per cubic meter	18–54 (avg 44)

TABLE 2.—*The Cladocera of Bull Shoals Reservoir*

Littoral:
- *Sida crystallina* (O. F. Müller)
- *Latona setifera* (O. F. Müller)
- *Simocephalus expinosus* (Koch)
- *S. vetulus* Schødler
- *S. serrulatus* (Koch)
- *Scapholeberis kingi* Sars
- *Eurycercus lamellatus* (O. F. Müller)
- *Camptocercus rectirostris* Schødler
- *Kurzia latissima* (Kurz)
- *Leydigia quadrangularis* (Leydig)
- *L. acanthocercoides* (Fischer)
- *Alona rectangula* Sars
- *Pleuroxus denticulatus* Birge
- *Chydorus globosus* Baird
- *C. spaericus* (O. F. Müller)

Limnetic:
- *Leptodora kindtii* (Focke)
- *Diaphanosoma leuchtenbergianum* Fischer
- *Daphnia ambigua* Scourfield
- *D. galeata* Sars *mendotae* Birge
- *D. parvula* Fordyce
- *D. retrocurva* Forbes
- *D. schødleri* Sars
- *Ceriodaphnia lacustris* Birge
- *C. quadrangula* (O. F. Müller)
- *Bosmina longirostris* (O. F. Müller)

sities of approximately 37/liter throughout the remainder of the year. Copepods decline from densities of approximately 9/liter in the spring to 0.6/liter in late summer.

Sampling Procedure

Plankton samples were taken at three stations representing the lower, middle, and upper main-stream areas (fig. 1) beginning in April 1964 and continuing through August 1967. Intervals between sampling were approximately 4 weeks except at the middle reservoir station where samples were taken each week from March 1967 through August 1967.

Vertical distribution and diurnal vertical movements were determined from 100-liter samples pumped from 3- to 6-meter intervals, surface to the bottom, using an electric well pump delivering a flow of 31 liters per minute. Samples were concentrated by passing the flow through a No. 20 silk bolting cloth plankton net.

Population density, structure, and dynamics were determined from samples taken by oblique tows with metered Miller samplers fitted with No. 10 nets. Sample size ranged between 2,000 and 6,000 liters/tow. Replicate tows showed no significant differences.

Larval and fry fish, primarily threadfin shad, *Dorosoma petenense*, were sampled with Miller townet samplers, meter nets, and midwater trawls at the middle reservoir station during the spring and summer of 1967. Digestive-tract contents were analyzed to determine when these fish became daphnid predators and to compare predation with *Daphnia* mortality.

Water samples were taken with pumps and Kemmerer water bottles and were analyzed for seston content after zooplankton was removed. Seston standing crops were used as an index of available food for *Daphnia*.

Sample Analysis

Plankton samples were concentrated or diluted to fixed volumes, and 1-milliliter subsamples were withdrawn and placed in counting cells. All organisms were counted in two to four 1-milliliter subsamples with a 30× binocular microscope.

Samples taken at the middle reservoir station from March through August 1967 were used for examining dynamics of the populations. *Daphnia* were identified to species, counted, and measured. Measurements were made from the base of the spine to the anterior extension of the carapace. All of the eggs and embryos in each subsample were counted, and the number in each brood pouch was recorded. Photographs of life stages were taken with a 35-mm camera mounted on a binocular compound microscope. Calculations of vital statistics of *Daphnia galeata mendotae* followed the method described by Edmondson (1960) for rotifers and applied by Hall (1964) to *D. galeata mendotae* and by Wright (1965) to *D. schødleri*. The following calculations are required:

- (N) number of *Daphnia* per liter.
- (E) number of eggs and embryos per liter.
- (D) egg and embryo duration in days.
- (B) finite birth rate (number of newborn per individual per day).
- (N_o) initial population number.
- (N_t) population number after time t.
- (b) instantaneous birth rate.
- (r) population change rate.
- (d) death rate.

$$B=\frac{E}{DN_o}$$

$e^b=1+B$ solve for b

$e^{rt}=\frac{N_t}{N_o}$ solve for r

$r=b-d.$

Egg and embryo time duration is the most difficult factor to determine. The duration of time for embryonic development is dependent on temperature (Hall, 1964). It was not possible to compute values of D for the daphnids in each different temperature stratum, since the population exhibited extensive vertical migration throughout the 37-meter depth. The maximum density of adults generally occurred in the metalimnion, and the majority of those below the metalimnion were observed to migrate into it at night. The temperature at the depth where maximum density occurred was chosen to base calculations of D. The eggs and embryo duration was then determined from a graph constructed from the data of Hall (1964).

Digestive tracts from fish larvae and fry were teased apart on microscope slides, and the contents were identified and counted at 30× and 100× magnification.

Seston standing crops were estimated by wet combustion with potassium dichromate as an oxidant (Maciolek, 1962).

Daphnia galeata mendotae

SEASONAL CYCLE

Population estimates for *D. g. mendotae* show a single-peaked curve (monocyclic) for each of the three reservoir areas (fig. 2). The population was monacmic in 1965 and 1967 with the single maximum occurring in the spring or early summer of each year followed by decline and collapse in the summer. The population was diacmic in 1966 with the spring maximum followed by a minor late summer pulse and collapse in the fall and winter. Within any one of the three annual cycles, the population maintained detectable densities at the lower reservoir station 2 or 3 months longer than at the upper station and approximately 1 month longer than at midreservoir.

The first individuals (fig. 3) appearing in February and March were juveniles recruited from resting eggs (fig. 4). These individuals appeared when the water temperature was 7° C. and began releasing parthenogenetic eggs (fig. 5) approximately 21 days later when the water temperature was 14° C. The ex-ephippio generation gave rise to subsequent generations (fig. 6) which developed maximum densities in April, May, and June. Maximum densities ranged between 4,133 and 16,199 per cubic meter at the lower reservoir station, 4,987 and 14,640/m³ at the middle station and 2,336 and 4,277/m³ at the upper station. Males (fig. 7) appeared in April or May at a ratio of 1 to every 21

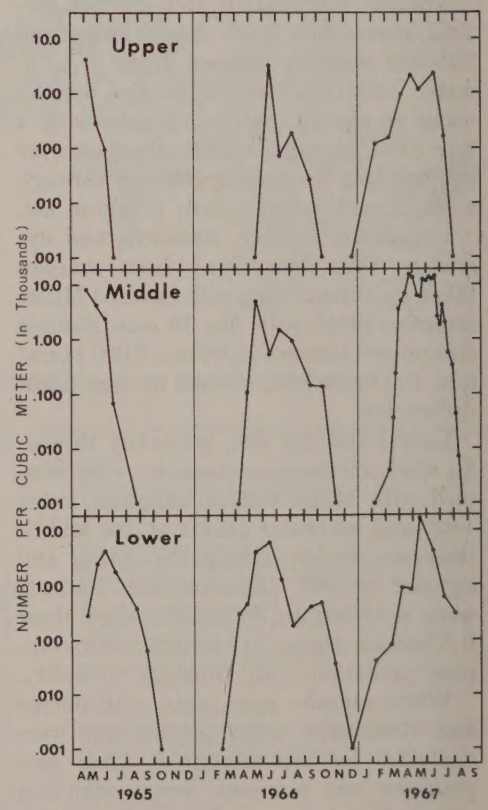

FIGURE 2.—*D. g. mendotae* abundance at three areas of Bull Shoals Reservoir.

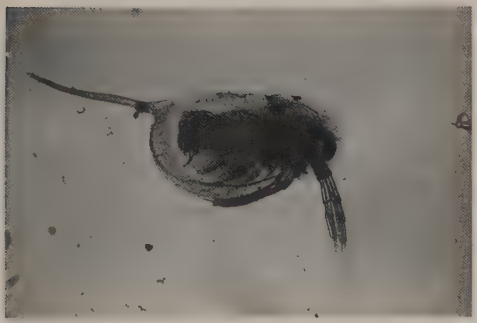

FIGURE 3.—Ex-ephippio juvenile *D. g. mendotae* from Bull Shoals Reservoir March 3, 1967.

FIGURE 5.—Parthenogenetic eggs being released into the brood chamber of *D. g. mendotae*.

adult parthenogenetic females. Females bearing ephippia also appeared at a ratio of 1 to every 21 adult parthenogenetic females.

VERTICAL DISTRIBUTION AND MIGRATION

Adult *D. g. mendotae* inhabited almost all depth strata in the spring, with the maximum density generally at 12 meters at midday (fig. 8). Juveniles occurred in the strata overlying the adults with the maximum density generally at 6 meters. Adults and juveniles occurred at greater densities at 24 meters and 18 meters respectively in the summer, before population collapse. Occasionally adults departed from their usual pattern of depth distribution at midday and showed maximum densities in the deepest strata.

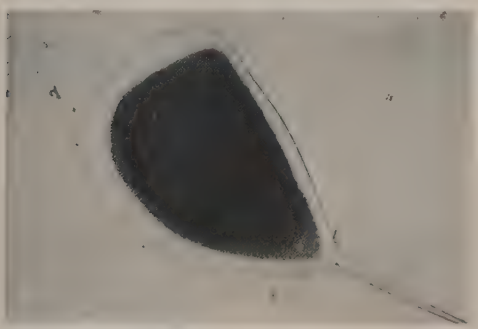

FIGURE 4.—*D. g. mendotae* ephippium from Bull Shoals Reservoir April 24, 1967.

Most adults migrated at night from the lower hypolimnion into the upper strata (clinolimnion), while the juveniles were observed to dissipate from the mid-epilimnion into the surface waters and the metalimnion (fig. 9). The population of adults was rather uniformly distributed at 1300 hours from 3 to 33 meters with a slight concentration in the lower half of the water column. At 1800 hours the animals had moved slightly upward so that there was a slightly greater concentration in the mid-depths, with none having been taken below 30 meters. Adults were still absent from the surface waters. By midnight the bulk of the population was above 12 meters, and adults were nearly as abundant at the surface as at 12 meters, the depth of maximum abundance. Adults had begun their descent at sunrise. Most of the juveniles were distributed at 1300 hours from 3 to 9 meters. At 1800 hours the juveniles had moved slightly upward and downward, and by midnight the bulk of the population was from 6 to 12 meters.

POPULATION DYNAMICS

Population data for *D. g. mendotae* at the middle reservoir area in 1967 are shown in table 3. Densities increased rapidly from a trace on March 10 to an estimated 14,514/m^3 on April 24 (fig. 10). This initial increase was due to large clutch sizes

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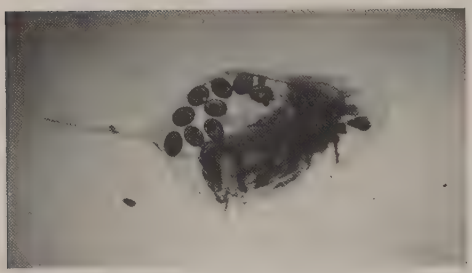
Adult, April 4.

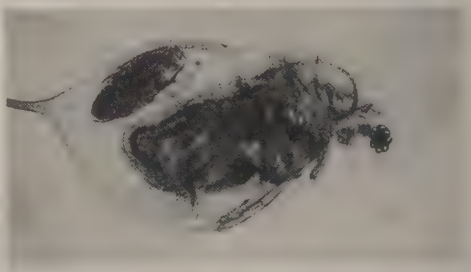
Adult, July 1.

Juvenile, April 4.

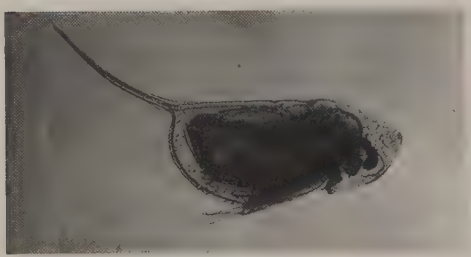
Juvenile, July 1.



Adult, May 17.



Adult, August 5.



Juvenile, May 17.

Juvenile, August 5.

FIGURE 6.—Adult and juvenile *D. g. mendotae* from Bull Shoals Reservoir.

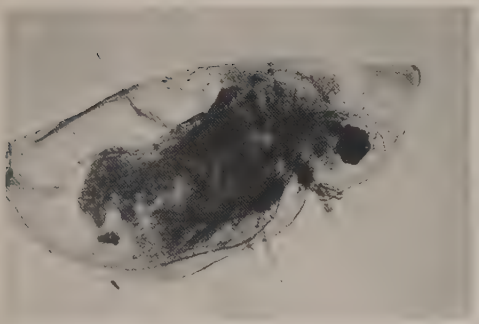


FIGURE 7.—*D. g. mendotae* male from Bull Shoals Reservoir May 5, 1965.

rather than high numbers of reproductive adults. The increase preceded the spring phytoplankton pulse, and the data indicate a lack of food to sustain the population density. A decline in density on May 12 and 17 coincided with an extremely low seston standing crop estimate of 0.04 mg C/liter. The mean number of eggs and embryos per adult showed a decrease from 5.3 on April 6 to 0.7 on April 29, and the death rate (fig. 11) increased sharply on April 29 before the marked decline. The birth rate and the population-change rate (fig. 12) declined and then showed increases as the population density increased on May 20.

Hall (1964) demonstrated that food level affects reproduction of *D. g. mendotae* through the number of young per brood. The brood size is determined by the abundance of food. Hall found that food levels did not affect the lifespan and reported that previous experiments by Banta et al. (1939) showed an increased longevity at near-starvation food levels. It may then be concluded that the decrease in brood size of the Bull Shoals Reservoir population on April 24 and 29 was a result of a diminished food supply. The declining birth rate and population-change rate on April 29 reflect this.

The increased death rate observed on April 29 cannot be attributed to starvation as evidenced by Hall (1964) but must be attributed to some other agent. A comparison of the carapace lengths of adults (fig. 13) and the number of young per brood (fig. 14) shows that reproductive adults had attained maximum size at the same time as the food level and the resulting number of young per brood reached minimums. These large individuals were the first generations produced in early April. The increasing death rate on April 29 indicates that natural death of these large individuals may have become

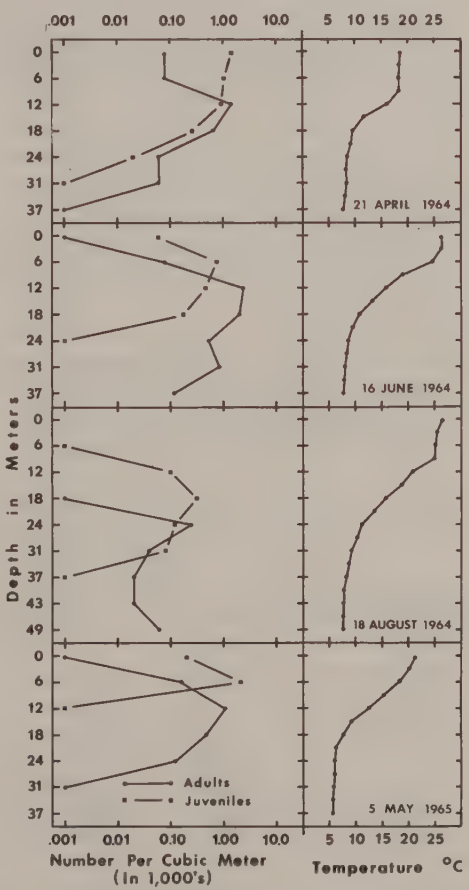


FIGURE 8.—Selected diagrams comparing seasonal depth distribution of *D. g. mendotae* adults and juveniles with temperature profiles in Bull Shoals Reservoir.

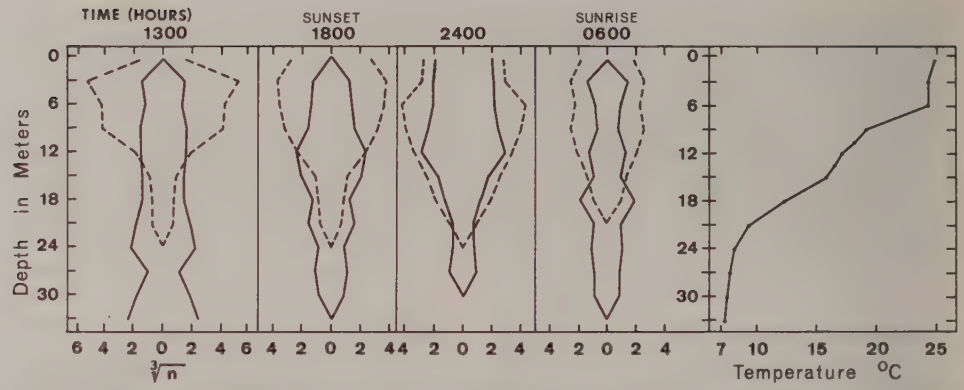


FIGURE 9.—Vertical distribution of *D. g. mendotae* adults (solid lines) and juveniles (broken lines) at 1300, 1800, 2400, and 0600 hours in Bull Shoals Reservoir on June 7–8, 1967. Densities plotted as the cube root of the numbers per liter.

significant. Death from old age would have been insignificant while the population was young and expanding. The high death rate of older individuals and the low birth rate observed on April 29 resulted in the population density minimum observed on May 12 and 17.

The increase in density on May 20 coincided with the spring pulse of net phytoplankton, *Dinobryon divergens*, *Asterionella*, *Fragilaria*, and *Melosira*. The seston standing crop increased sharply from the low of 0.04 mg C/liter in April to 0.32 mg C/liter on May 16. The mean numbers of eggs and of embryos per adult increased threefold, but the numbers never attained the size of those observed for the initial population pulse. The second population maximum was more a result of greater numbers of reproductive adults and shorter embryonic development time than of large clutch sizes.

TABLE 3.—*Population data for* D. g. mendotae, *1967*

Date	No./M³	Eggs and embryos/M³ (N)	Eggs and embryos per adult	Embryonic development in days (D)	Finite birth rate (B)	Instantaneous birth rate (b)	Population change rate (r)	Death rate (d)
March 10	5	0	0					
18	36	0	0					
25	242	0	0					
31	3,510	2,718	4.3	8	0.10	0.10	+0.06	+0.04
April 6	5,110	5,877	5.3	8	.14	.13	+.03	+.10
15	6,716	4,785	4.2	7	.10	.10	+.09	+.01
24	14,514	4,380	1.6	6	.05	.05	−.02	+.07
29	13,495	1,844	.7	6	.02	.02	−.24	+.26
May 12	6,219	4,704	2.1	4	.19	.17	0	+.17
17	6,186	1,874	2.1	4	.08	.07	+.24	−.17
20	12,648	8,234	2.2	4	.16	.15	0	+.15
27	12,389	4,063	1.8	4	.08	.08	+.02	+.06
June 3	13,864	2,768	.7	4	.05	.05	−.03	+.08
7	12,347	1,658	.7	4	.03	.03	+.03	0
13	14,640	1,977	.8	3	.05	.04	−.23	+.27
17	5,828	1,323	.4	3	.08	.07	−.12	+.05
24	2,511	1,168	1.3	3	.16	.14	−.04	−.10
July 1	1,834	1,535	1.5	3	.28	.25	+.12	+.13
8	4,261	906	.7	3	.07	.07	−.10	+.17
15	2,092	1,270	1.2	3	.20	.19	−.18	+.37
22	572	191	.8	3	.11	.11	−.08	+.19
29	333	229	.9	2.5	.28	.24	−.29	+.53
Aug. 5	43	7	.5	2.5	.07	.06	−.26	+.32
12	7	0	0					
18	0	0	0					

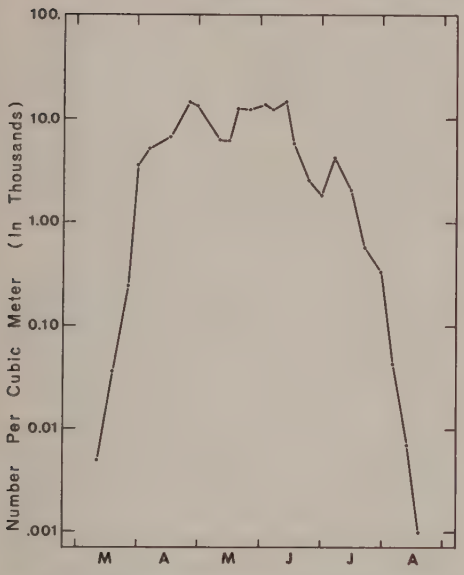


FIGURE 10.—Population density of *D. g. mendotae* at the middle area of Bull Shoals Reservoir, March 10–August 12, 1967.

The population maintained its second maximum until June 13 and then declined until no detectable population remained on August 18. The decline and eventual collapse of the *D. g. mendotae* population coincided with a population increase of the predatory cladoceran, *Leptodora kindtii* (fig. 15) and increased utilization by young-of-the-year threadfin shad (fig. 16). The mortality rate declined as the

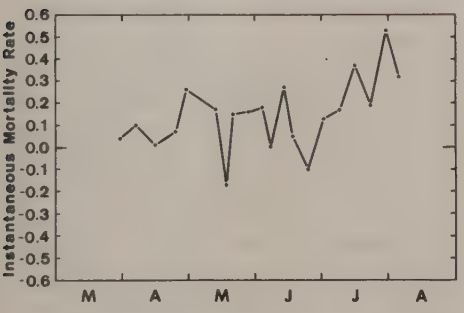


FIGURE 11.—Instantaneous mortality rates of *D. g. mendotae* in 1967.

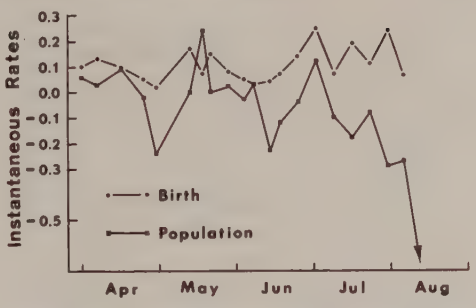


FIGURE 12.—Instantaneous birth rates (b) and population change rates (r) of *D. g. mendotae*.

population density of *Daphnia* began decreasing, but showed a marked increase at the time the *Leptodora* population attained a density of 154/m³ and young-of-the-year shad became significant predators.

Threadfin shad were introduced in Bull Shoals Reservoir in 1961 and were taken in small numbers in 1962 in cove rotenone samples (unpublished data from Robert Baker, Arkansas Game and Fish Commission). In the late summer of 1965 the population had expanded to an estimated 21,800 young-of-the-year per hectare (8,820/acre) (Houser and Dunn, 1967). Crustacean densities in 1965 declined from an estimated high of 46.5/liter in May to a low of 2.4/liter in August, indicating that intensive predation may have resulted in extremely low populations of crustaceans during the summer (Applegate and Mullan, 1967b). Population estimates of young-of-the-year threadfin shad

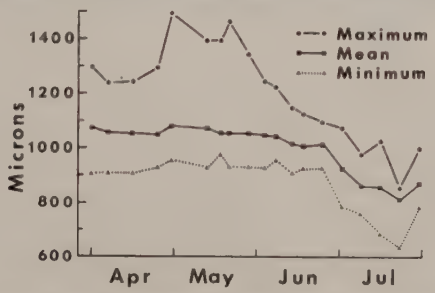


FIGURE 13.—Carapace length of reproductive adult *D. g. mendotae* at Bulls Shoals Reservoir.

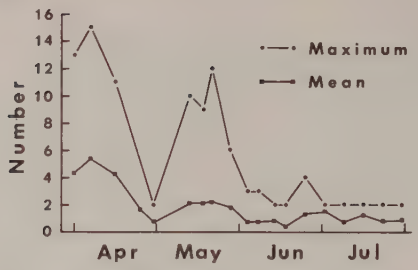


FIGURE 14.—Number of young per brood of reproductive adult *D. g. mendotae* at Bull Shoals Reservoir in 1967.

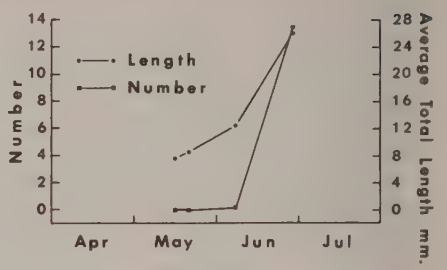


FIGURE 16.—Average number of *D. g. mendotae* in the digestive tracts of young-of-the-year *Dorosoma petenense* and average length of *D. petenense* young.

in June and July 1966 were 33,110/ha (13,400/acre) and 19,400/ha (7,850/acre) respectively, but a late summer estimate of 13,200/ha (5,340/acre) indicated a year class density decrease of 39 percent from the late summer estimate in 1965 (Houser and Bryant, 1967). Estimates in August 1967 indicated a population density of 10,070/ha (4,075/acre), representing a decrease of 54 percent from 1965 (Houser, unpublished).

The first threadfin shad larvae captured in 1967 were taken on May 15, when they ranged between 4.0 and 14.0 mm in total length. The food of the larvae consisted primarily of subadult copepods ranging between 181 and 373 microns in length (table 4). The first *D. g. mendotae* appeared as juveniles in the digestive tracts of threadfin shad ranging between 14.0 and 16.5 mm in total length on June 7. Both juvenile and adult *D. g. mendotae* were major food items of threadfin shad ranging between 15.0 and 37.0 mm in total length on June 28. *Leptodora* was also included in the diet of shad ranging between 35 and 37 mm in total length on the latter date. Threadfin shad ranging in length between 30 and 50 mm in July and August showed a selectiveness for large zooplankters (Baker, 1968).

White crappie (*Pomoxis annularis* Rafinesque) young also were captured on June 7, 1967, when they ranged between 5.0 and 14.0 mm in total length. *Daphnia galeata mendotae* made up 5.8 percent by number of the organisms in the digestive tracts (table 4) of young greater than 8.0 mm in total length. Although white crappie as well as other fishes contributed to the total crustacean mortality, their contribution was certainly not as important as that of threadfin shad.

That threadfin shad predation was a major cause of the *Daphnia* population decline and subsequent collapse is suggested by the ascending death rates following the population maximum of *Leptodora*. In July and August the average *Daphnia* birth rate was greater than that of the preceding months but the population density and the population change rate showed continual negative trends until no detectable population remained.

The food level as indicated by seston standing crops was estimated at 0.33 and 0.46 mg C/liter in July and August, re-

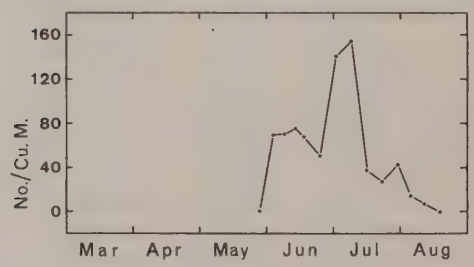


FIGURE 15.—Population density of *L. kindtii* at middle area of Bull Shoals Reservoir in 1967.

TABLE 4.—*Food of larval and fry threadfin shad and white crappie at middle station of Bull Shoals Reservoir in daylight hours, selected dates in 1967*

	Threadfin shad						White crappie	
	May 15–20		June 7		June 28		June 7	
Total mean length—millimeters	8.1		12.4		26.2		8.1	
Total length range—millimeters	4.0–14.0		8.0–16.5		15.0–37.0		5.0–14.0	
Number examined	32		50		32		50	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Food items:								
Aphanocapsa	1	1.3						
Anacystis					9	0.6		
Pediastrum					61	3.8		
Stephanodiscus	14	17.9	4	1.7			16	4.1
Dinobryon					1	.1		
Codonella					9	.6		
Rotifera	2	2.6	98	41.9	662	41.5	148	38.2
Copepoda nauplii	37	47.4	3	1.3			4	1.0
Copepoda	22	28.2	114	48.7	366	22.9	114	29.4
Bosmina	2	2.6	4	1.7	49	3.0	83	21.5
Leptodora					7	.4		
Alona			1	0.4				
D. galeata mendotae			10	4.3	433	27.1	22	5.8
Total	78	100.0	234	100.0	1,597	100.0	387	100.0

spectively. These values indicate a larger potential food source at the time of population decline than during the population maxima. The number of young per brood declined following the spring pulse of net phytoplankton and maintained an average of approximately one throughout June and July.

Both the mean and the minimum carapace lengths of reproductive adults began decreasing on July 1 and trended downward as the population declined (figs. 6 and 13). Brooks (1965) reported that a decrease in size of reproductive adults is to be expected. From an analysis of the observations by Hall (1964) on food level and carapace size, Brooks (1965) generalized that cyclomorphic species tend to be larger at the onset of maturity when the assimilation rate is high because of high temperature or abundant food and if there is not a large, rapidly growing helmet. The carapace of an individual with a large, rapidly growing helmet will be smaller at the onset of maturity than will that of an individual with a small, slow-growing helmet.

The decreasing carapace lengths of reproductive adults in Bull Shoals Reservoir coincided with rising water temperatures and increased helmet growth. The decrease in body size also coincided with young-of-the-year threadfin shad predation. Brooks (1965) theorized that the development of large transparent helmets and small body size when water temperatures are rising and fish predation is increasing are adaptations which decrease the prey's chances of being eaten. The small size increases the chance that the individuals of the first adult instars will reproduce. A decrease in maximum carapace length from 1,491 microns on April 29 to 854 microns on July 22 indicates that predation was heavy upon larger individuals through June and July in Bull Shoals Reservoir.

Brooks and Dodson (1965) observed significant differences in lake plankton populations where alewife, *Alosa pseudoharengus* and glut herring, *Alosa aestivalis*, had sizable populations. *Daphnia* species were never dominant in lakes having *Alosa* whereas they were always dominant in lakes void of *Alosa*. The elimination of large pelagic crustaceans by *Alosa* allowed the primarily littoral species, such as *Bosmina longirostris* to spread into the pelagic zone. The smallest mature females of *Daphnia* were considered too large to have a reasonable chance of surviving *Alosa*

predation long enough to produce sufficient young.

The smallest mature female *D. g. mendotae* were likewise unable to survive threadfin shad predation in the middle area of Bull Shoals Reservoir during the late summer of 1967. The greater densities and the longer annual cycles of *D. g. mendotae* in the lower reservoir area suggests that greater water depth acts favorably for survival of the species. Whereas *Daphnia* inhabit all depth strata, shad inhabit only the upper strata during the warmer months (Houser and Dunn, 1967).

The observation by Brooks and Dodson (1965) that *Bosmina longirostris* replaces *Daphnia* when fish predation is selective for large Crustacea is also true for Bull Shoals Reservoir. *B. longirostris* is the dominant planktonic crustacean throughout almost all seasons. Its density is inversely related to that of *Daphnia* within the reservoir. The density of *B. longirostris* is greatest in the upper reservoir areas where *Daphnia* population densities are smallest (Applegate and Mullan, 1967b). A comparison of *B. longirostris* densities at the middle reservoir station (fig. 17) shows that the maximum densities occurred in the spring as did those of *D. g. mendotae*, but *B. longirostris* maintained a population during the summer and fall when *Daphnia* populations were nondetectable or extremely low.

Differences in the annual cycles of *D. g. mendotae* and *B. longirostris* at the middle reservoir area may reflect differences in predation between years. In 1965, when threadfin shad densities were at a maximum (21,800 young-of-the-year per hectare) *D. g. mendotae* densities showed a rapid decline in the spring and no detectable population throughout the remainder of the year. *Bosmina*, the dominant crustacean, occurred at low densities ranging between 590 and 2,250/m³ during the sum-

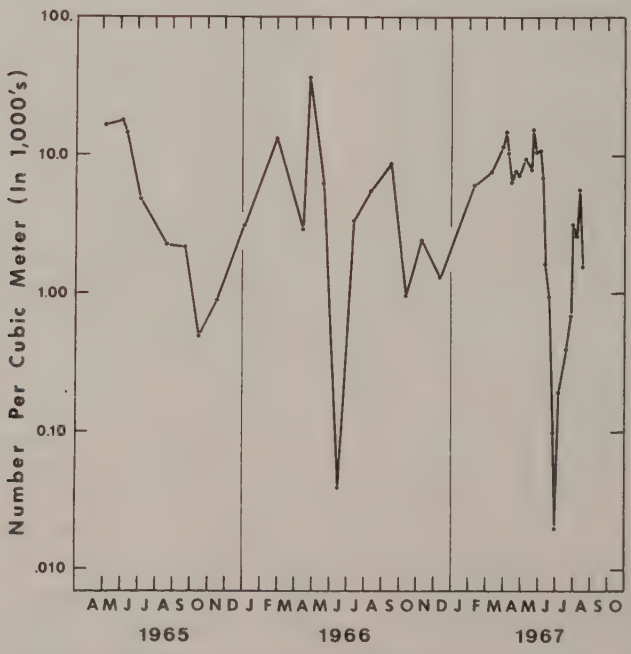


FIGURE 17.—Population density of *B. longirostris* at the middle area of Bull Shoals Reservoir.

mer and fall. *Leptodora* was a trace in 1965 summer population estimates and would have contributed an insignificant amount of predation on other Cladocera.

The 1966 decline in year class strength of threadfin shad may have been of sufficient magnitude to permit *D. g. mendotae* survival. *Daphnia galeata mendotae* and *Bosmina* densities declined in June at the time young threadfin shad would have included them in their diet. But following the June decline, *D. g. mendotae* maintained low densities ranging between 1,450 and 130/m³ throughout the remainder of the summer and fall. *Bosmina* increased in densities ranging between 3,300 and 8,600/m³ during the summer. *Leptodora kindtii* was again an insignificant species, appearing as a trace in population estimates.

The combined predation of *Leptodora* and threadfin shad appears to have been instrumental in causing the population collapse of *D. g. mendotae* in the early summer of 1967. Weaker year class strength of shad and a population increase of *Leptodora* were major differences in 1967 as compared with the previous years. Shad ingested food organisms of a size encompassing juvenile and adult *Daphnia* on June 28, and *Leptodora* attained a maximum density at approximately the same time. The combined predation of these two sources, which is reflected in *D. g. mendotae* death rates and population change rates, is also reflected in *Bosmina* density. *Bosmina* estimates show a decline from 15,340/m³ on May 20 to 20/m³ on July 1. *Bosmina* later increased to densities comparable to those in the spring after shad became more selective for larger food items, and *Leptodora* densities declined.

The large blue-green alga *Lyngbya birgei*, which pulses in the summer and fall in Bull Shoals Reservoir, becomes more important in the diet of threadfin shad during those seasons (Baker, 1968). *Lyngbya*'s acting as a buffer may be a major reason why the small crustacean *Bosmina* maintained relatively dense populations during the summer. Two other daphnids (*D. retrocurva* and *D. parvula*) also maintained populations in the late summer and fall.

Daphnia retrocurva and *D. parvula*

SEASONAL CYCLE

Population estimates of *D. retrocurva* and *D. parvula* show variation between years and reservoir areas (figs. 18 and 19). Maximum densities usually occurred in the early spring before those of *D. g. mendotae* and declined to negligible or low

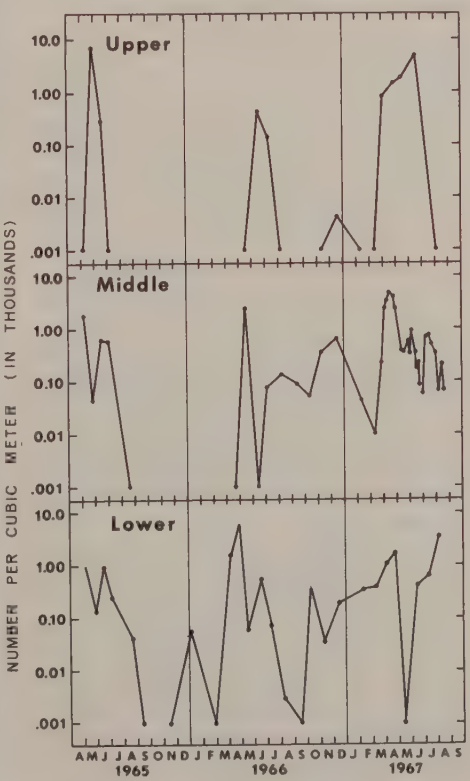


FIGURE 18.—*D. retrocurva* abundance at three areas of Bull Shoals Reservoir.

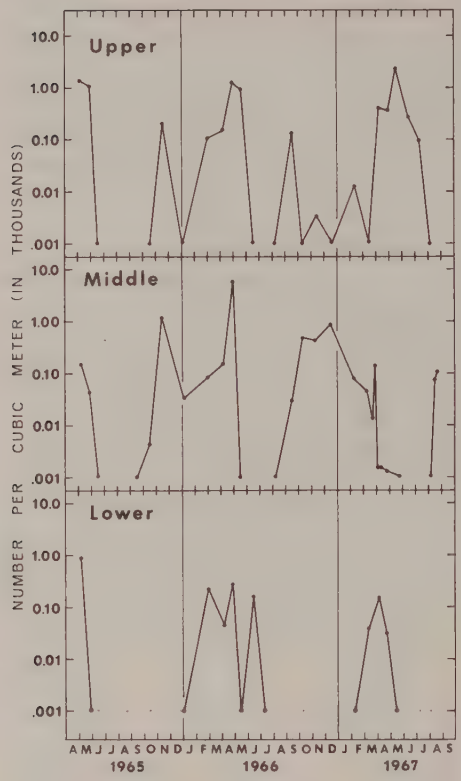


FIGURE 19.—*D. parvula* abundance at three areas of Bull Shoals Reservoir.

densities at the time *D. g. mendotae* densities were high. An increase in density of *D. retrocurva* or of *D. parvula* or of both usually followed the decline of *D. g. mendotae* in the summer and fall. *Daphnia retrocurva* and *D. parvula* showed rapid declines in density in the summer of 1965 and no detectable populations throughout most of the summer of that year, when threadfin shad densities were high.

Parthenogenetic reproduction occurred at all seasons. Males and ephippia (figs. 20 and 21) appeared in the late fall, winter, and spring.

VERTICAL DISTRIBUTION

D. retrocurva and *D. parvula* exhibited similar seasonal depth distributions at daylight hours (fig. 22). Juveniles occurred at greater densities in strata overlying the adults. Unlike *D. parvula* (fig. 23), *D. retrocurva* is a strongly cyclomorphic species. The amount of helmet growth is primarily dependent on water temperature and turbulence. Small helmets occur in individuals developing when water temperature is below 18° C., and large helmets occur when water temperature is above 18° C. (Brooks, 1946, 1964, 1965). A comparison of vertical distribution and helmet size of representative individuals (fig. 24) shows that the population density was usually greatest in strata where water temperature was less than 18° C. and that helmets were small. Population density was greatest in the epilimnion in June, and maximum helmet size was attained. In July and August the population retired to the hypolimnion, and most individuals again bore small helmets.

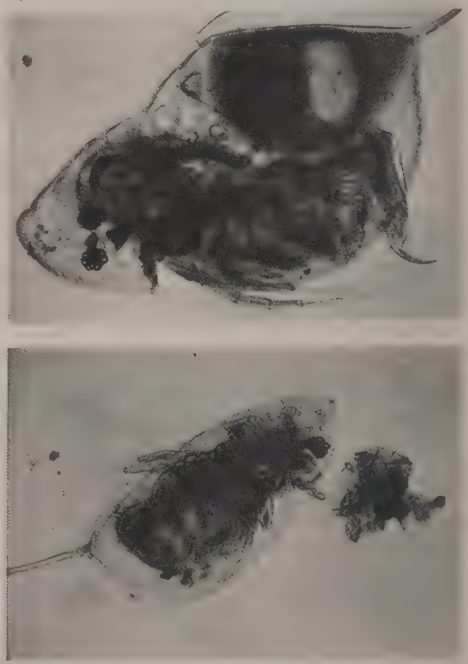


FIGURE 20.—Female bearing ephippium (above) and male (below) *D. retrocurva* from Bull Shoals Reservoir April 4.

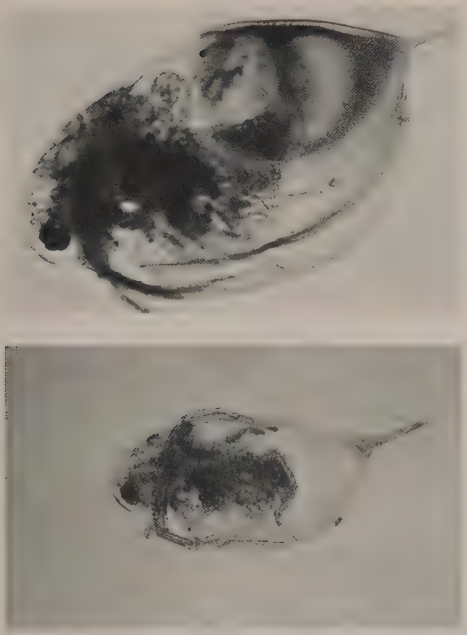


FIGURE 21.—Female bearing ephippium (above) and male (below) *D. parvula* from Bull Shoals Reservoir May 4.

The distribution of *D. retrocurva* in the hypolimnion during most of the summer and fall, and the uncommon occurrence of shad below the metalimnion, could significantly reduce fish predation during the warmer months. The collapse of the population in June 1965 at the middle reservoir area may reflect predation by the abundant shad population of that year. The collapse occurred at the time *D. retrocurva* occupied the epilimnion and was most vulnerable to predation.

Greater water depth appears to enhance the survival of *D. retrocurva* and *D. parvula* as it did for *D. g. mendotae*. Populations of *D. retrocurva* and *D. parvula* were negligible or extremely small at the shallow upper reservoir area throughout the summers, but were present throughout most of the summers in the deeper reservoir areas.

POPULATION DYNAMICS

Winter populations of *D. parvula* and *D. retrocurva* occurred together at the middle reservoir station in 1966. Reproduction was observed throughout the winter period, but densities of neither species exceeded 1,000/m³ until March 31, 1967. *Daphnia parvula* densities declined from the winter low and were negligible by April 1967, whereas *D. retrocurva* densities increased to an estimated 4,785/m³ on April 14 (fig. 18). A decline in density on May 12 coincided with the low food level estimate that adversely affected the *D. g. mendotae* population. The mean number of eggs and embryos per brood declined from 3.8 on April 6 to 0.1 on April 29, paralleling those of *D. g. mendotae*. The mean number of eggs and embryos per brood increased to 1.0 as the food level increased, but the population density did not exceed 1000/m³ throughout the remainder of the spring and summer. A decline from an estimated 946/m³ on June 3 to 60/m³ on July 1 coincided with the *Leptodora* population increase and the inclusion of larger zooplankton in the diet of young threadfin shad.

The trend of declining carapace length as helmet size increased was the same for *D. retrocurva* as for *D. g. mendotae*. The mean carapace length of reproductive females increased from 936 microns on March 31 and April 4 to 1,123 microns on May 27 and then declined to 832 microns on July 8.

Daphnia ambigua and *D. schodleri*

SEASONAL CYCLE

Daphnia ambigua appeared in population samples in the springs of 1965 and 1967 at the middle and lower reservoir areas (fig. 25). Densities never exceeded 200/m³, and ephippia (fig. 26) were present each time a population was observed.

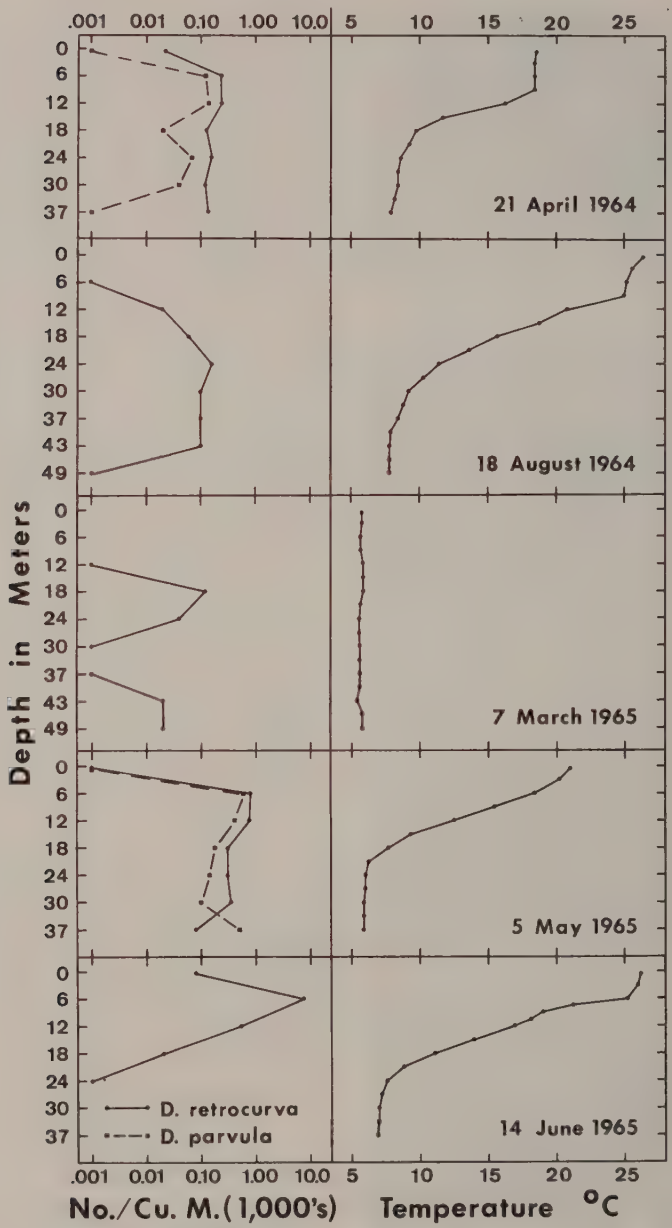


FIGURE 22.—Selected diagrams showing the seasonal depth distribution of *D. retrocurva* (solid line) and *D. parvula* (broken line) in Bull Shoals Reservoir.

Daphnia schødleri (fig. 27), the largest daphnid in Bull Shoals Reservoir, was not observed at the middle or the upper reservoir areas in 1965. Densities of less than 100/m^3 were estimated at the lower reservoir in the spring and fall of 1965. *Daphnia schødleri* became of increasing importance in population estimates of 1966 and 1967 as threadfin shad densities declined. Maximum densities of *D. schødleri* occurred in the spring and early summer, coinciding with those of *D. g. mendotae* and surpassing those of *D. g. mendotae* in April and June 1967 at the lower reservoir area. Resting eggs were produced in early summer, from which the population was recruited in the following winter and spring.

Daphnia schødleri densities at the middle reservoir area in 1967 declined from about 1,000/m^3 in June to nondetectable densities in August. The decline paralleled those of *D. g. mendotae*, *D. retrocurva*, and *Bosmina longirostris* and coincided with high *Leptodora* density and young-of-the-year threadfin shad predation.

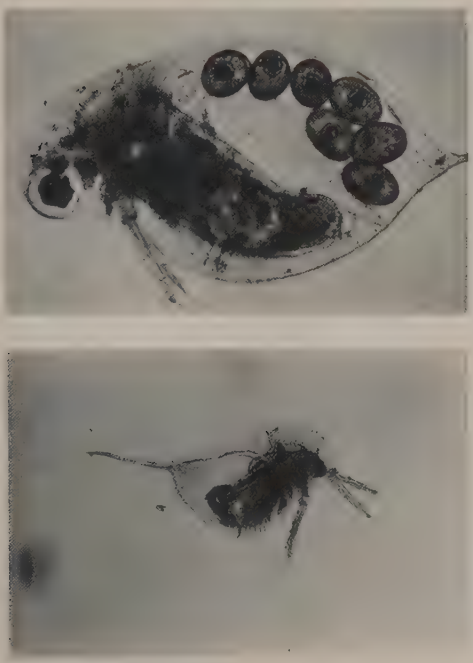


FIGURE 23.—*D. parvula* adult (above) and juvenile (below) from Bull Shoals Reservoir.

VERTICAL DISTRIBUTION AND MIGRATION

Daphnia schødleri behaved essentially as a cold-water form. The majority of adults were observed in the hypolimnion both day and night (fig. 28). No adults were taken above the 12-meter stratum at 1300 and 1800 hours. At 2400 hours some of the animals had moved upward to the 9-meter stratum and a few adults were taken at the surface. Juveniles occurred at all depths during the day, and those in the epilimnion migrated to the hypolimnion at night.

Although *Daphnia schødleri* is a pond species in western North America it is common in the plankton of Lake Mendota and the littoral areas in Great Slave Lake (Hutchinson, 1967). It is most abundant in the euphotic zone of Canyon Ferry Reservoir in Montana (personal communication from John C. Wright, Department of Botany and Bacteriology, Montana State University, Bozeman).

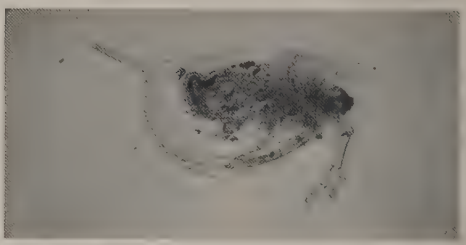
Hutchinson (1967) reported that the factors influencing the distribution of *Daphnia schødleri* are obscure, though in a large transparent body of water some feature that is significant to the animal is present in the littoral and absent from the depths. It is of interest that *Daphnia schødleri* appears to have developed as a cold-water form in the relatively transparent Bull Shoals Reservoir (average secchi disk transparency >3 meters).

Daphnia schødleri, because of its large size, is subject to intensive predation by adult and advanced fry fishes. Galbraith (1967) demonstrated a selectivity for *Daphnia* greater than 1.3 mm in size by rainbow trout (*Salmo gairdneri*). Hall (1964) observed that adult ciscoes (*Leucicythys artedi*) and black crappies (*Pomoxis nigromaculatus*) consumed the

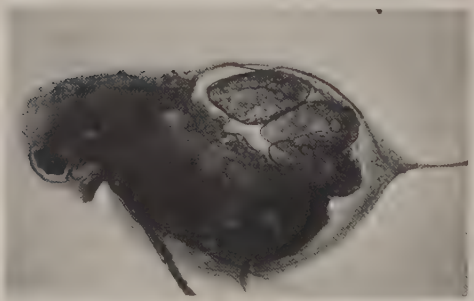
Adult, January 13.

Adult, March 9.

Juvenile, January 13.



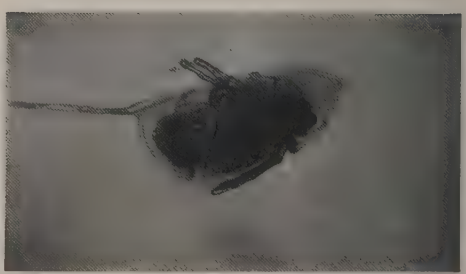
Juvenile, March 7.



Adult, February 7.

Adult, April 4.

Juvenile, February 7.



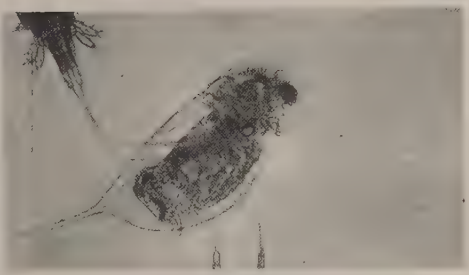
Juvenile, April 4.

FIGURE 24.—Adult and juvenile *D. retrocurva* from Bull Shoals Reservoir.

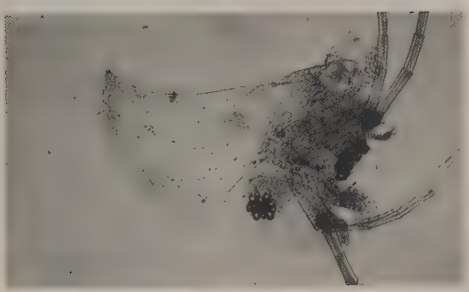
Adult, May 15.

Adult, July 11.

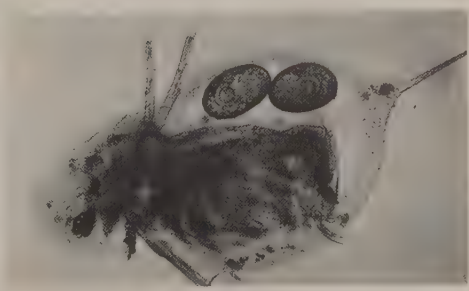
Juvenile, May 17.



Juvenile, July 11.



Adult, June 17.



Adult, October 10.

Juvenile, June 17.

Adult, November 9.

FIGURE 24.—Adult and juvenile *D. retrocurva* from Bull Shoals Reservoir—Continued.

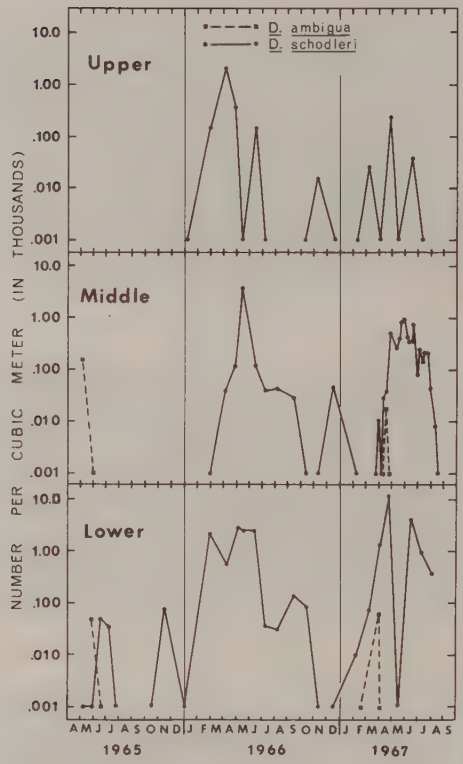


FIGURE 25.—*D. ambigua* (dashed lines) and *D. schødleri* (solid lines) abundance at three areas of Bull Shoals Reservoir.

large *D. pulex* but did not feed on the smaller *D. galeata mendotae*. Analysis of 506 rainbow trout stomachs collected from Bull Shoals Reservoir in the spring and summer of 1967 showed *D. schødleri* adults as the major crustacean consumed.

The selecting of large zooplankton by threadfin shad of less than 30 mm in total length and by other planktivorous fish could influence the vertical distribution of *D. schødleri* in Bull Shoals Reservoir. Prolonged annual cycles at the lower reservoir area and the absence of a population at the upper reservoir area in 1965, when shad densities were high, indicate that greater water depth is advantageous for survival. By adapting to the deeper strata, 18–49 meters, some of the reproductive adults are removed from the zone of intensive and differential fish predation. Such a vertical distribution could prolong the annual cycle and increase the chances for resting egg production. The elimination of *Daphnia* in Connecticut lakes by *Alosa* predation reported by Brooks and Dodson (1965) occurred in lakes having mean depths ranging between 4 and 7 meters and maximum depths less than 21 meters.

Summary

Maximum population density of daphnids in Bull Shoals Reservoir occurred in April, May, and June. Populations declined to insignificant densities throughout the remainder of the year. Declines coincided with the inclusion of *Daphnia* in the diets of threadfin shad of less than 14.0 mm. Declines in the summer of 1967 coin-

FIGURE 26.—*D. ambigua* females and ephippia from Bull Shoals Reservoir, April (above) and May (below).

FIGURE 27.—*D. schødleri* adult (above) 33x and juvenile (below) from Bull Shoals Reservoir.

cided with both young threadfin shad predation and high *Leptodora* density.

Population changes associated with declining year class strength of threadfin shad were, essentially, an increase of large *D. schødleri* and *Leptodora kindtii* from nondetectable or trace densities to relatively large populations, an increase in daphnids in summer from nondetectable densities to detectable densities, and a twofold to threefold increase in summer standing crops of *Bosmina longirostris*.

Three main types of *Daphnia* life histories were exhibited in Bull Shoals Reservoir. *Daphnia galeata mendotae*, *D. schødleri*, and *D. ambigua* were aestival species. Individuals appeared sporadically in the late winter or early spring and attained maximum densities in the spring and early summer. Resting eggs were then produced, from which the populations were recruited in the following winter and spring. *Daphnia parvula* was also an aestival species, but individuals appeared in the late summer and multiplied to produce

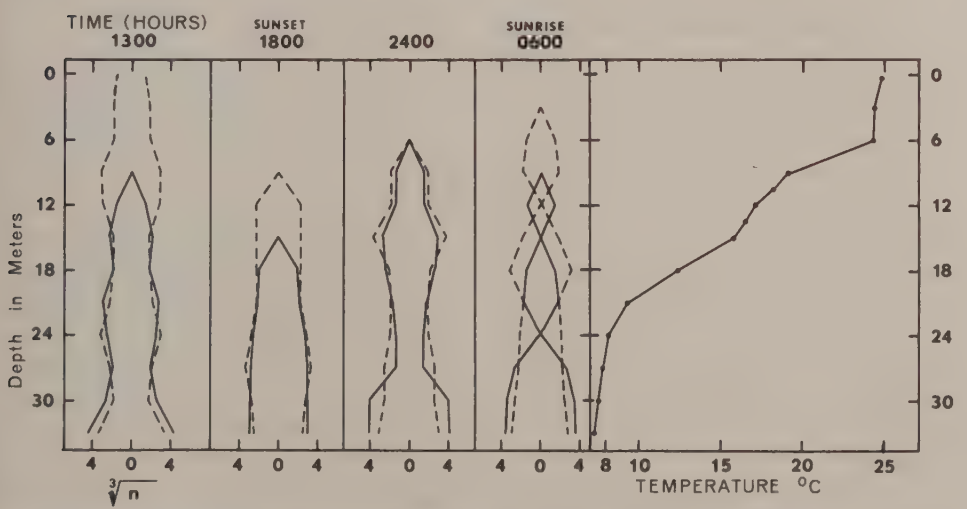


FIGURE 28.—Vertical distribution of *D. schødleri* (solid lines) and juveniles (broken lines) at 1300, 1800, 2400, and 0600 hours in Bull Shoals Reservoir on June 7–8, 1967. Densities plotted as the cube root of the number per liter.

maximum densities in the fall, winter, and early spring. Resting eggs were produced, from which the population was recruited in the following late summer. *Daphnia retrocurva* tended to be a perennial species. Parthenogenetic reproduction occurred at all seasons, but both types of behavior, overwintering and oversummering of adult females, and production of resting eggs in the fall, winter, and spring, occurred. All daphnids were aestival each year at the shallower upper reservoir area where populations were absent during the warmer months. The production of resting eggs by each of the five species tends to eliminate the chances of extinction by threadfin shad predation.

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